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**A Fossil Ray,  
Possibly *Myledaphus*  
(Elasmobranchii: Batoidea)  
from the Late Cretaceous  
Oldman Formation  
of Western Canada**

by Wann Langston, jr.



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## Résumé

Cette étude décrit le squelette partiel d'un poisson batoïde des dépôts d'eau douce de la formation Oldman. Les lacunes du squelette reliées à sa ressemblance apparente à celui des guitares et des raies compliquent sa classification. Même la dimension et la forme originales de l'animal demeurent très imprécises. Toutefois, à la lumière d'indices accidentels, plutôt négatifs, on est porté à croire que le spécimen serait un *Myledaphus*.

## Summary

A partial skeleton of a batoid fish obtained from freshwater deposits of the Oldman Formation is described in this paper. The incompleteness of the skeleton, combined with its superficial resemblances to banjo fish, skates, and rays, hampers attempts to define its generic affinities. Even the original size and shape of the fish cannot be precisely determined. It appears, however, from a combination of circumstantial and "negative" evidence, that the specimen may belong to *Myledaphus*.



## Biographical Note

Dr. Wann Langston, a leading researcher into the evolution of fossil reptiles, is particularly known for his work on dinosaurs. While he was Curator of Fossil Vertebrates with the National Museums of Canada from 1955 to 1962, Dr. Langston collected dinosaur remains from southern Alberta and Saskatchewan, and he has worked under contract for the Museums studying horned dinosaurs. He has published major works on crocodile evolution and primitive reptiles and has contributed numerous articles to scientific journals. Now Vertebrate Paleontologist with the Texas Memorial Museum and Director of the Vertebrate Paleontology Laboratory, the University of Texas, Austin, Dr. Langston is collecting in Big Bend National Park near the Mexican border.



## Introduction

It is well known that owing to their lack of a bony skeleton, elasmobranch fishes are represented in the fossil state mainly by teeth, denticles, and various dermal spines. Only occasionally and under exceptional circumstances are the primarily cartilaginous portions of the skeleton preserved as, for example, at Mt. Lebanon, in the lithographic stone of Bavaria and at Cérin, Monte Bolca. With the notable exception of the pleuracanth such occurrences are practically unknown in freshwater deposits. The only non-dental elasmobranch skeletal material hitherto reported from such deposits in western Canada is the posterior part of a vertebral column from the late Cretaceous Edmonton Formation, called *Palaeospinax ejuncidus* by Lambe (1918). The discovery of a partial skeleton of a batoid fish in the Oldman Formation of southeastern Alberta is therefore not without interest.

The specimen was found by Charles M. Sternberg in 1937, 6½ miles southeast of the town of Manyberries. The locality is about 11 miles northwest of the site where in the same year Dr. Sternberg obtained the exceptional skeleton of *Paratarpon apogerontus* recently described by Bardack (1970). Interestingly, these are the only fish skeletons of any degree of completeness ever reported from the Oldman beds. Although at first glance the present specimen appears unusually well-preserved, detailed examination and comparison leave so much uncertainty about the affinities of the fish that one can only speculate about its probable generic assignment.

## Acknowledgments

I am indebted to Dr. Dale Russell of the National Museums of Canada for permission to complete this study, commenced over a decade ago when I was associated with the Museum of Natural Sciences. Dr. C.M. Sternberg has been most helpful with comments about the occurrence of the fossil. Dr. Rainer Zangerl of the Field Museum kindly provided the radiographs of the specimen, reproduced here as positive prints. Drawings are by Mrs. Doris Tischler.



Plate 1

Photograph of incomplete batoid skeleton NMC 12443 partly excavated in the field. Dark spots adjacent to specimen, first believed to be remains of the skin, do not

contain any x-ray opaque materials, and are probably of carbonaceous origin. Scale is in inches. Photograph by C.M. Sternberg, NMC negative 83383.

According to the field records, the specimen (NMC 12443) was found about 30 ft below the top of the Pale Beds [i.e., Oldman Formation], in a sandstone with clay and lignitic bands near the base of a sandstone butte, on the west side of a coulee tributary to South Manyberries Creek, in SW¼, sec. 35, tp. 4, rge. 5 west of the 4th meridian (see Canada Dep. Mines and Res. Geol. Map 567A—Dunmore, Alberta).

The specimen comprises the anterior part of the axial skeleton including chondrocranium, the ankylosed synarcual plate, and an articulated series of 28 definable "free" vertebrae. The animal lay on its ventral surface with the vertebral column curved distally to the left (Plate 1). The head is distorted, but some vertebral centra are uncrushed. Preservation was such that preparation in a conventional manner was impossible, and most of the study had to be carried out with the aid of radiography. After removal of the field jacket and some matrix the upper side of the block containing the specimen was imbedded in bee's wax reinforced with gauze and then x-rayed (Plate 2). This procedure revealed that the visceral and appendicular skeletons are missing. No teeth or dermal denticles are preserved. Weathering evidently destroyed the posterior part of the skeleton before its discovery.



Plate 2

Radiograph positive of NMC 12443: left-hand page, anterior part of skeleton; right-hand page, posterior part. Scale: length of bar = 5cm.



Plate 2 (cont'd.)



Plate 3

Detail of radiograph positive print of NMC 12443 showing tesserae investing part of the calcified cartilage in the area of the vertebral ankylosis. Scale: 1.6 actual size.



All preserved parts of the skeleton are composed of calcified cartilage. The anterior parts are largely invested by isometric tesserae<sup>1</sup> of up to 2 mm in diameter, and are clearly seen in the radiographs. Tesserae in the head region do not appear to be arranged in any particular pattern, but those in the pectoral area show a distinct longitudinal orientation (Plate 3).

The general outline of the chondrocranium is interpretable from the radiograph. Its length of 21 cm is about 1.6 times its width. A large orbital vacuity can be seen to occupy the middle part of the right side of the specimen. Pre- and post-orbital areas of the skull appear to have been about equal in size, the width posteriorly being only a little more than that in front. As preserved, the cranium is truncated anteriorly; there is no evidence that a rostrum was present, but the possibility cannot be completely ruled out. Wide olfactory capsules, evidently deflected downward in batoid fashion, are clearly seen (Figure 1, n). These are separated medially by a gap of about 10 mm. Outlines of the antorbital (dorsal) fontanelle are indistinct, although a certain "thinness" in the radiograph indicates its general position. The opening was evidently about half as long as the cranium and more oval than triangular in outline. A light area postero-medial to the right orbit occupies the position of the otic capsule on that side. A distinct process projecting anterolaterally from behind each olfactory capsule (Figure 1, a) was probably for attachment of the antorbital cartilage, of which no trace is preserved. A triangular process projecting posterolaterally from either side of the otic region

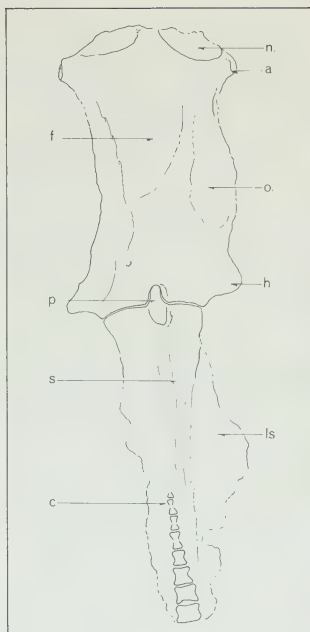


Fig. 1. Diagrammatic representation of anterior part of the skeleton. a, process for attachment of antorbital cartilage; c, primary double cone; f, area of anterior fontanelle (distorted); h, hyomandibular process; ls, ? lateral stay; n, olfactory capsule; o, orbit; p, "odontoid" process of ankylosis; s, ? synarcual spine (displaced).

(Figure 1, h) no doubt gave attachment to the hyomandibular cartilage. There is no evidence of a postorbital process. The cranio-cervical joint is more than half as wide as the chondrocranium. It comprises two thick articular facets separated by a deep U-shaped notch, which receives a corresponding tongue-like process of the ankylosis.

The vertebral column consists anteriorly of a massive synarcual ankylosis, a series of fused vertebrae, which characteristically supports the pharyngobranchial cartilages and some pectoral

<sup>1</sup> The word used here in the sense of Woodward (1889) should not be confused with the same term sometimes applied to the tessellated pattern of dermal bones in ostracoderms.

structures in skates and rays. This is followed by 28 movable postankylosis vertebrae. The part of the column preserved may therefore represent no more than half the body length.

The ankylosis, clearly defined in the radiograph (Plate 2), is a little longer than the skull. It broadens anteriorly at its articulation with the braincase, where it attains a maximum width of 74 mm. The massive cranial condyle bears a strong median "odontoid" process (Figure 1, p). Seven vertebral centra, the first represented by only the posterior half of the double cone, appear at the posterior end of the ankylosis. Although these centra do not differ greatly in length from those in the free column their diameters decrease rapidly craniad, so that the width of the first centrum is only about one-quarter that of the eighth, or first postankylosis, vertebra. There is no indication of laterally expanded vertebral arcualia behind the main area of consolidation. Lateral processes of any kind are ill-defined, and I am unable to distinguish any areas of attachment for the branchial cartilages. A narrowly triangular, longitudinal ridge seen a little to the right of the midline in the radiograph (Figure 1, s) is perhaps the displaced synarcual spine (see Garman 1913, pl. 55). No sign of an articulation for the scapular arch can be seen. What may be remains of a "lateral stay" appears as a wide triangular area on the right side of the ankylosis.

All post-ankylosis vertebrae have simple spool-shaped centra with thickened articular edges (Plate 2). Double cones are not discernible in the radiographs of this series. Viewed in the horizontal plane, the centra appear fairly uniform in shape and dimensions: those just behind the ankylosis have a maximum transverse diameter of about 16 mm, a least diameter of 15 mm, and a length of about 12 mm, whereas at the end of

the preserved column, these measurements are 17.5, approx. 14, and 11 mm respectively. Irregular shadows along the sides of the centra represent the distorted and fragmentary remnants of the tesserate covering of the arcualia.

A systematic tool used by some in elasmobranch studies is the pattern of calcification in the vertebral centra (for a recent review of the limitations of this "system," see Applegate 1967). To expose this pattern a centrum is sectioned transversely at its narrowest diameter; according to Ridewood (1921) such sections are most reliable in closely related taxa if they are obtained from caudal vertebrae. However, no caudal elements being available in the present specimen, a well-preserved and easily removed mid-trunk vertebra (the second behind the ankylosis) was selected for sectioning.

This vertebra has a tiny (diameter: 0.9 mm) chordal canal. The subcircular centrum is of relatively massive and uncomplicated form (Figure 2). It is constructed of tightly appressed, concentric lamellae (= lines or zones of growth (Ridewood 1921)). Regularly alternating hard and soft calcified zones are of fairly regular thickness (approx. 0.28 mm). Some 24 of them occur along the transverse radius of the centrum. Although they parallel the irregular outlines of the centrum peripherally, these annulae become more regularly circular toward the chordal canal. The cellular composition characteristic of the outer zone of the chordal sheath (see Applegate 1967) is clearly discernible in the annulae at a magnification of X10. A dark band about 0.3 mm wide occurs a short distance from the chordal canal. This is composed of denser material than the "zones of growth" and evidently represents the middle zone of the sheath cartilage, that is, the "double cone" of authors. Within this, and sur-

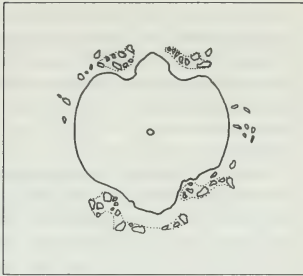


Fig. 2. Diagrammatic cross-section of the second post-ankylosis vertebra, at midlength. Actual size. Small irregularly disposed objects are calcified tesserae.

rounding the chordal canal, is a lighter and less compact inner zone representing the calcified elastica interna.

The broad lateral, and relatively narrower dorsal and ventral lobes of the cross-section are presumably formed by the coalescence of expanded horizontal and vertical calcified rays (toward the distal end of the preserved column longitudinal shadows on the radiograph suggest the presence of better-defined calcified septa). The only evidence of uncalcified intermedialia (*sensu* Ridewood) are the notches in the sides of the centrum. Calcified tesserae occupy these notches, which were sites of persistently cartilaginous arch components.

The fish described above was a large one, but in the absence of fins and the tail, conclusions about its proportions are only speculative. Living stingrays, for example, vary from fishes with relatively wide disks and short tails (butterfly rays) to species with whiplash tails three times the length of the body. If this fish was similar to the moderately long-tailed *Dasyatis hastatus*, the animal may have been about 3 metres long. It was, however, smaller than individuals of several existing dasyatid species.

The thoroughly calcified vertebral centra and the absence of a postorbital process are clear evidence that the Alberta fish belongs to the modern level of elasmobranch organization (Schaeffer 1967). The laterally expanded and downwardly deflected nasal capsules, the strong condyloid occipital articulation, and the massive ankylosis are exclusive batoid qualities. In most other respects the specimen offers a puzzling array of features commonly found among banjo fish (Rhinobatoidea), skates (Rajoidea), and rays (Myliobatoidea).

Absence of a rostrum would favour assignment to the rays, but it would not rule out inclusion with the skates—the existing *Malacorhina* lacks a rostral cartilage. The orientation of the nasal capsules seems more ray-like than skate-like, but the general shape and proportions of the rather narrow skull are reminiscent of some skates (especially *Malacorhina*) and guitar fish, minus the rostrum. The resemblance to rhinobatoids is accentuated by the absence of a postorbital process. This process, either relict or secondarily developed, is generally present in existing rays although it has no jaw-supporting function. It is usually fragile and often only narrowly attached, so it is possible that the process may have been destroyed in the fossil.

In so far as it is interpretable the ankylosis, with what is believed to be a wide lateral stay, resembles that of *Rhinobatus percellens* (Garman Pl. 55, fig. 4). Neither is it so long and slender as in the rays *Aetobatus* and *Rhinoptera*, nor does it widen anteriorly as in *Potamotryon*, or *Dasyatis*. It is, however, longer and narrower than in *Raja*. Absence of an obvious scapular articulation at the side of the ankylosis suggests that the scapulae were joined to its upper spine in simple skate fashion

rather than by the complicated lateral articulation found in rays. But if this was the natural state of affairs, it may represent a primitive condition.

Hasse (1879-1885) based a comprehensive system of elasmobranch classification upon the arrangement of secondary calcification seen in the longitudinal septa of the vertebral centra. Opinion differs with respect to the usefulness of this feature. Regan (1906) and Ridewood (1921), for example, have attacked the "system" as being inapplicable at higher taxonomic levels, but Applegate (1967) finds it valid within certain limitations. The patterns of secondary calcification ("stars") revealed in transverse sections of the centra may not be reliable keys to phylogenetic inferences, and according to Ridewood (p. 396) they "do not appear to have any direct bearing on the classification of the families" within the Batoidea. Nevertheless, lacking more definitive criteria, I shall note some aspects of vertebral structure that may be helpful in analyzing the systematic position of the Oldman fish.

The outstanding feature of the centrum described above is its compactness as compared with most elasmobranch vertebrae. Although a basic rayed pattern can be detected, the appearance is completely different from the many-branched "star" found in *Raja rhinobatus*, believed to have the most generalized caudal vertebrae among batoids (*sensu* Romer 1966, less torpedinoids), is considered in some detail by Ridewood. The calcification pattern is said to vary among certain species from a distinct eight-rayed star to a compact pristid-like structure, and some variation also occurs ontogenetically. The eight-rayed star in caudal vertebrae of *R. granulatus* gives way anteriorly to more simplified patterns as a result of enlargement and coalescence of the calcified

septa. It is easy to imagine the fossil fitting into interspecific, ontogenetic or metameric series such as these, and its high degree of calcification is no doubt partly a reflection of its anterior position in the column.

Similar variations occur also among the dasyatid stingrays where instances of excessive calcification are reported (Ridewood 1921; Hasse 1885). The fossil vertebra could theoretically be derived from the patterns illustrated for the rays *Rhinoptera javanica* and even *Urogymnus* (= *Rhachinotus*) *asperimus* or *Myliobatis neuhoi* (see Ridewood 1921, figs. 36, 37). Indeed the sectioned centrum appears fairly similar to a caudal vertebra of "Trygon" figured by Hasse (1882, Pl. 19, fig. 3), and is even more like one ascribed to a Cretaceous *Rhinoptera* (Hasse, Pl. 21, fig. 29).

The foregoing analysis reveals such basic uncertainties and ambiguities that systematic determination below the ordinal level is very uncertain. Though clearly a batoid, the fish was certainly not a pristid or a torpedo. The vertebral structure apparently argues against assignment to the Rajidae, and the absence of a rostral cartilage (if natural) against the Rhinobatoidea, as understood from most of the existing representatives.

Collectors have long been aware that scattered teeth of a ray, *Myledaphus bipartatus* Cope, are ubiquitous in the predominately freshwater Oldman and Edmonton Formations in western Canada. Indeed so abundant are they that virtually every fossiliferous concentration of any variety will be found to contain these double-rooted, polygonal crushing teeth. The genus is usually placed among the Dasyatidae. No other kinds of ray teeth have ever been reported from the same deposits. There is thus some circumstantial support for

supposing that the skeleton just described belongs to *Myledaphus*, and it is disappointing that the lack of teeth in the specimen precludes a positive statement. In sum, what evidence there is favours a reference to either the guitarfishes or to the ray families Rhinopteridae or Dasyatidae. I have opted for the latter, because of the possibility that the skeleton may belong to *Myledaphus*.

Most extinct batoid taxa are based on teeth and denticles, and the present specimen cannot, of course, be compared with these. Some, mostly older taxa, whose skeletons are known, are so primitive as to show stronger resemblances to selachians than to the Alberta ray. The batoid affinities of the Jurassic *Asterodermus*, *Belemnobatis*, and *Spathobatis* are still disputed (see Saint-Seine 1949; Schaeffer 1967). More advanced types, mostly representing living genera, are among the magnificent assemblage of Eocene elasmobranchs from Monte Bolca. Unfortunately, despite their generally impressive state of preservation, the skulls and vertebrae are not adequately revealed in the material described by Jaekel (1894). Useful comparisons with the Alberta specimen are therefore impossible. Similar difficulties arise in attempting to compare the Cretaceous material from Mt. Lebanon, in which batoids are richly represented (Hay 1903; Woodward 1942).

Among Canadian elasmobranchs, the poorly preserved caudal skeleton provisionally assigned to *Palaeospinax* by Lambe apparently represents a selachian having "cyclospondylic" vertebrae and densely clothed by a shagreen of tiny granular tubercles. The fish was probably considerably smaller than the Oldman ray.

As noted, there is no basis for comparisons with *Myledaphus*, to which genus the specimen may well belong.

Although it may be of no significance in relation to present questions, the following note is of some interest in connection with *Myledaphus*. In spite of the great abundance of this presumed dasyatid ray's teeth in the Oldman, Edmonton, and other similar late Cretaceous and early Tertiary deposits, I am unaware of the discovery anywhere in these beds of a characteristic

myliobatoid tail spine ("stinger"), so demanding of respect in living stingrays. Admitting the hazards of negative "evidence," it nevertheless seems reasonable, in view of the incredible numbers of their teeth, to suppose that the extinct rays were devoid of such spines. Some living myliobatids and the dasyatid *Urogymnus* lack stingers.

The sedimentary character of the rocks surrounding the specimen suggests an area of swash, and the first idea that came to mind regarding the mode of burial was that the fish had been stranded on a tidal flat. But such sedimentary structures can also result from seasonal flooding in rivers and lakes; nearby exposures at the same horizon contained the fragmentary plant and vertebrate (mostly hadrosaurian) remains that are most often associated with fresh and brackish water depositional environments.

It is assumed that as in most rays the individual possessed dermal denticles; the absence of these in the fossil, together with loss of jaws and fins, indicates that maceration was far advanced at the time of burial. Shadows seen on the radiographs of the chondrocranium suggest wrinkles, which may have existed before burial and which could have been caused by desiccation. These conditions recall a singular characteristic of the decomposition of rays sometimes observed on modern beaches. Such fish when stranded may come to rest with their broad ventral surfaces flat against the substrate. The mouth and pharyngeal cavity soon fill with sediment which has the effect of anchoring the carcass while the fins disintegrate. The skin on the superior surface is soon reduced by scavengers and maceration (under salt water conditions a combination of pickling and desiccation usually delays complete degradation of the skin and total loss of its denticles). Currents and animal activities may then separate the axial skeleton from the jaws and gill arches, which are held fast in the sediment occupying the branchial chamber. By this time very little connective tissue remains and the cartilaginous skeleton is largely exposed to drying and consequent shrinking and warping, particularly of the chondro-



cranium. Hence, isolated jaws with teeth and axial skeletons comprising crania and parts of spinal columns may be buried separately. This course of events seems adequate to explain the occurrence of the Oldman ray.

Discovery of a representative of a largely marine group of fishes in sediments that may be of non-marine origin calls for some comment. A general description of the geological conditions in the Manyberries district of Alberta is given by Russell and Landes (1940: 62-72). As elsewhere the Oldman deposits in this area are presumed to be mainly of freshwater origin. They contain freshwater invertebrates, dinosaurs, other reptiles, and mammals. However, the marine Bearpaw beds occur stratigraphically only a short distance above the fossil horizon, and proximity to marine waters at the time of the ray's burial is implicit in the inferred late Cretaceous history of the region (see Williams and Burk 1964).

The appearance of a fossil elasmobranch under such conditions should occasion no surprise and should not be taken as a contraindication of a freshwater origin for the deposits adduced from other evidence. Smith (1936) offers a list of 52 Recent species of elasmobranchs that have been reported from fresh water. Although later work (Bigelow and Schroeder 1953) suggests that some of these records are erroneous, there is still ample justification for Smith's statements (p. 65) that "we are not entitled to exclude the elasmobranchs from fresh water on physiological grounds. Given the proper ecological conditions, there is little doubt that most of the smaller forms, at least, could survive as well in fresh water as in the ocean."

There can be no question about the occurrence of *Myledaphus* in non-marine sediments in western Canada and elsewhere. Restriction of this genus to North America supports the notion that it was confined in fresh to brackish

water.<sup>2</sup> Interestingly among existing elasmobranchs the rays seem to have the widest tolerance for non-saline environments, and one family, Potamotrygonidae, is restricted to fresh water. Other rays are said to occur commonly in shoal channels and lagoons along tropical coasts, in waters of variable salinity. Similar conditions may be reasonably inferred from the thinly laminated siltstones and interbedded carbonaceous shales that surrounded the present specimen.

Rays at the present time have a mostly tropical to subtropical distribution; only a few species range regularly into temperate latitudes. Occurrence of the ray skeleton in rocks that also contain crocodilian remains indicates a climatic range consistent with that of existing species.

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<sup>2</sup> The striking external resemblance between the teeth of *Mylodaphus* and the mainly Old World Cretaceous-Recent *Hypolophus* has been noted by several authors. However, McNulty (1964) reports significant histological differences in the structure of the crowns by which these fishes can be distinguished.



## References

### Applegate, S.P.

(1967). A survey of shark hard parts. In *Sharks, Skates and Rays*, ed. by Perry W. Gilbert and others. Baltimore, Johns Hopkins Press. 37-67, 7 figs., 4 pls.

### Bardack, D.

(1970). A new Teleost from the Oldman Formation (Cretaceous) of Alberta. *Natl. Mus. Canada Publ. in Palaeontol.* No. 3. Ottawa.

### Bigelow, H.B. and W.C. Schroeder.

(1953). Fishes of the western North Atlantic, Part 2—Sawfishes, Guitarfishes, Skates and Rays. *Mem. Sears Found.* 1: 588pp.

### Garman, S.

(1913). The Plagiostomia (sharks, skates, and rays). *Mem. Mus. Comp. Zool. Harvard*, 36: 528pp.

### Hasse, C.

(1879-1885). *Das natürliche System der Elasmobranchier auf Grundlage des Baues und der Entwicklung ihrer Wirbelsäule*. Jena. 3 vols. 1879: 6 + 76; 1882: 6 + 284; Suppl. 1885: 27p.

### Hay, O.P.

(1903). On a collection of Upper Cretaceous fishes from Mount Lebanon, Syria, with descriptions of four new genera and nineteen new species. *Bull. Amer. Mus. Nat. Hist.* 19: 395-452.

### Jaekel, O.

(1894). Die eocänen Selachier vom Monte Bolca. *Ein Beitrag zur Morphologie der Wirbelthiere*. Berlin, Kgl. Akad. der Wissenschaft. 176pp.

### Lambe, L.M.

(1918). On remains of a selachian from the Edmonton Cretaceous of Alberta. *Ottawa Nat.* 32 (2): 27-28.

### McNulty, C.L.

(1964). Hypolophid teeth from the Woodbine Formation, Tarrant County, Texas. *Ecl. Geol. Helvetiae* 57, (2): 537-539.

### Regan, C. Tate.

(1906). A classification of the selachian fishes. *Proc. Zool. Soc.*—1906, (48): 722-758.

### Ridewood, W.G.

(1921). On the calcification of the vertebral centra in sharks and rays. *Phil. Trans. Roy. Soc. London* (B), 210: 311-407.

### Russell, L.S. and R.W. Landes.

(1940). Geology of the southern Alberta Plains. *Geol. Surv. Canada Mem.* 221: 223pp.

### Saint-Seine, P.

(1949). Les poissons de calcaires lithographiques de Céron. *Nouv. Arch. Mus. Hist. Nat. Lyon* 2: 357pp.

### Schaeffer, Bobb.

(1967). Comments on elasmobranch evolution. In *Sharks, Skates and Rays*, ed. by Perry W. Gilbert and others. Baltimore, Johns Hopkins Press. 3-35.

### Smith, H.W.

(1936). The retention and physiological role of urea in the Elasmobranchii. *Biol. Rev.* 11 (1): 49-82.

### Williams, G.D. and C.F. Burk.

(1964). Upper Cretaceous. In *Geological History of Western Canada*, ed. by R.G. McCrossan and R.P. Glaister, Alberta Soc. Petrol. Geol.: 169-189.

### Woodward, A.S.

(1942). Some new and little known Upper Cretaceous fishes from Mount Lebanon. *Ann. Mag. Nat. Hist.* 9 (11): 537-568.





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